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THE COLORS OF NORTHERN GAMOPETALOUS
FLOWERS.¹

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THE Gamopetalæ are characterized by the more or less united petals. This series is not derived from the Choripetalæ, but represents an independent though parallel line of development. The union of the petals has not been induced by insects, and "is not," says Gœbel, "the result of a cohesion of originally free parts, but is due to the excessive growth of the zone of the floral axis in which the rudiments of the petals are inserted." Much uncertainty prevails as to the phylogeny of the gamopetalous series, which can only be settled by further investigation. There are two points of culmination. By common consent the Compositæ are placed at the head of this series and of the plant kingdom. In this family it is the community of flowers rather than the individual flower that is of chief importance. A secondary culmination occurs in the Labiatæ and Scrophular-

¹The Colors of Northern Monocotyledonous Flowers, *Amer. Nat.*, vol. xxxiii, p. 493; The Colors of Northern Apetalous Flowers, *Amer. Nat.*, vol. xxxv, p. 197; The Colors of Northern Polypetalous Flowers, *Amer. Nat.*, vol. xxxvi, p. 203.

iaceæ, families in which the flowers are zygomorphous and often of large size. It has been suggested that these two divisions represent two distinct lines of development and are of very different origin. The Compositæ are derived through the Rubiaceæ and Caprifoliaceæ from the Umbelliferæ, while the aroids are assigned as the remote ancestors of the labiate forms. It seems better, however, to regard the series as homogeneous. The gamopetalous families probably had a common starting point and are derived from a group of primitive forms allied to the progenitors of the Choripetalæ, but a later offshoot, and still retaining affinities with the monocotyledons. The flowers are characterized by definiteness in the number of parts and by their frequent cohesion, characters, says Engler, which must have become fixed at a very early period in their history. The Gamopetalæ are of later occurrence in the fossil state than the Choripetalæ.

The first of the gamopetalous orders, the Ericales, which includes six families, is the most primitive in structure. The flowers have the corolla lobed or pointed, or the petals may be entirely distinct; the ovary is superior except in the Vacciniaceæ; there are two typical staminal whorls, and the carpels equal the petals in number. In the genera *Clethra* and *Pyrola* the petals are but slightly, or not at all united, and in *Monotropa* and *Ledum* are regularly separate. Of the 81 flowers belonging to these six families 47 are white and 24 are red; while only 1 is yellow, 6 purple, and 3 green.

The Pyrolaceæ are low perennials with clustered evergreen leaves, growing in woodlands and swamps. The flowers are racemose and 7 of the species are white, 2 red, 1 purple and 1 green. They vary but little in size. Several of the white flowered species of *Pyrola* are tinged with green, while in *Moneses* and *Chimaphila* the white flowers are often pinkish. The purple *Pyrola uliginosa* is a bog plant. The flowers of this family are visited by bees, flies and beetles. The primitive color was doubtless greenish-white, which has varied into pink and purple. Flowers of different sizes have been observed on *P. minor*.

The Monotropaceæ are saprophytes without chlorophyll, and

with the leaves reduced to bracts. The plants which live in rich woods are white or colored with anthocyan. *Monotropa uniflora* (Indian pipe or ghost-flower) is usually pure white, and stands out in strong contrast with the dark brown soil of its woodland home. Occasionally the whole plant is pink or red. Specimens in drying turn black. *M. hypopitys* has the entire plant pale yellow, with yellowish or pink flowers. On the island of Wollin Knuth saw a bumblebee sucking the flowers. The plant of *Monotropis* is pale pinkish brown with fragrant pink flowers.

The flowers of the Ericaceæ are produced in great profusion, and often display bright masses of color, which are visible at a long distance. This family reaches its highest development in the temperate zones, the structure and form of the plants enabling them to endure the severities of alpine summits. The heaths proper are most abundant at the Cape of Good Hope, where more than 400 species have been described. Of the 38 northern species 22 are white, 1 yellow, 10 red, and 5 purple.

Some of the handsomest of the wild flowers belong to the genus *Azalea*. Of the five northern species two are white, one orange and two rose color, and all have large flowers with slender tubes. *A. lutea* (*A. calendulacca*) in spring is covered with orange flowers which turn to flame color. In the Alps on a hot June day the hillocks projecting from the surrounding snow are densely carpeted with the crimson flowers of the smaller and more primitive *A. procumbens* over which flit numerous bees and butterflies. Florists offer hybrids of *A. pontica* from Asia Minor, which display a great range of yellow and red coloring. Closely allied to the *Azaleas* and equally beautiful are the *Rhododendrons*. The flowers are red or purple, or in *R. maximum* rose or sometimes white spotted with orange, and are fertilized by bumblebees. *Rhododendron maximum* and *Kalmia latifolia* have been called the two handsomest North American shrubs. Bigelow remarks in his *Medical Botany* that "these shrubs, in luxuriant size and vigor, are seen to cover tracts of great extent, at one season presenting an unbroken landscape of gorgeous flowers." Asa Gray in one of his letters speaking of the glorious view from Roan Mountain, North Carolina, writes, "The valleys and mountains all around, covered with rich forest,

are adorned with *Rhododendron maximum* and *Kalmia latifolia* in immense abundance and profuse blossoming, of every hue from deep rose to white, and here and there among other shrubs *Asalca calendulacca*, of every hue from light yellow to deepest flame color." ¹ The flowers of *Kalmia* are red or red purple and are pollinated by bees. In northern New England the commonest species of *Kalmia* is *K. angustifolia*, which produces its crimson flowers in late spring. The central flowers of the corymb are smaller and imperfectly developed; the corolla is white and without pouches, while the stamens stand erect and are not exceeded in length by the pistil. Most of the northern genera of the Ericaceæ, however, are shrubby plants with small, white, racemose or clustered, drooping flowers attractive to the honeybee and bumblebees. Such are *Andromeda*, *Leucothoë*, and *Gaultheria procumbens*, or the checkerberry. The flowers of this last species are partially concealed beneath the leaves and in the grass and moss, amid which the plant grows. Yet I have found the honeybee and three species of bumblebees very frequent visitors. The aromatic scented flowers are white with reddish calyx and peduncles. It would be difficult to find greater extremes in conspicuousness than is presented by the magnificent color masses of *Rhododendron* and *Kalmia*, and the small concealed flowers of *Gaultheria*, yet these latter do not want for pollinators. None of the true heaths (*Erica*) are endemic in America, but two species (*E. cinerea* and *E. tetralix*, adventitious from Europe) occur in small patches on the Island of Nantucket. *E. carnea* unlike most red flowers of this family is adapted to butterflies. Both the petals and sepals are pink or crimson, and the peduncles are still more intensely colored. The inverted flowers were doubtless first adapted to bees, as is usually the case with campanulate flowers in this position. The entrance to the corolla has now become so narrowed that only the slender proboscis of the butterfly is admitted. Müller saw a bumblebee in vain striving to suck the honey. In the Alps he found it frequently visited by *Vanessa cardui*.

Of the Vacciniaceæ, or huckleberry family, 10 species are

¹Letters of Asa Gray, vol. ii, p. 692.

white, 11 red, and 2 green. The primitive color of the corolla seems to have been green, as it is still greenish, greenish-white, greenish-pink, or yellowish-green in the genus *Vaccinium*. The flowers are bell-shaped and the pollinators are bees. *V. pennsylvanicum* (the common blueberry) is white often tinged with red on the side exposed to direct sunlight. At the time of blooming in spring the leaves are reddish, and patches of these bushes on a hillside are visible at a long distance. The flowers of *Gaylussacia resinosa*, or the huckleberry, are red, and the entire plant exhibits a marked tendency to develop red coloration. The floral bracts and stems are reddish, and the leaves when stung by a gall-fly turn a deep red, while the brilliant crimson of the foliage in autumn is unsurpassed. The nodding flowers are visited, according to my observations, by nine species of bees besides several butterflies. If the entrance to the corolla, which is already quite small, should be further narrowed to the exclusion of bees, as has been described in *Erica carnea*, this species would become also adapted to butterflies. It might then readily be assumed that the red coloration had been produced in response to the visits of these insects, whereas it has arisen very early in the history of this flower independently of any supposed preference for this color which butterflies may possess. This the writer believes to have actually happened in the case of not a few red butterfly flowers. Conclusions as to the influence of insects in developing particular colors, it is evident, must be made with great caution. No other gamopetalous families contain so many red flowers as the Ericaceæ and Vacciniaceæ. In the development of red and the exclusion of blue coloring they resemble the Rosaceæ. But in fruit blue and blue black are in the Vacciniaceæ of common occurrence.

In the Primulales there are also two staminal whorls, and distinct petals still occur. The Primulaceæ contain 4 white, 11 yellow, and 7 red flowers. *Trientalis*, *Lysimachia*, *Steironema*, and *Anagallis* are pollen flowers and contain no nectar. The corolla is small and rotate. The white *Trientalis americana*, (star-flower) grows in damp woodlands, and is rarely visited by insects. *Anagallis arvensis*, or poor-man's weather-glass, has scarlet flowers, which are sometimes white, and in the variety

corulca are blue. The closing of the flower in the afternoon effects fertilization in the absence of insects. The species of *Lysimachia* and *Steironema* are yellow sometimes with a red center, or dark spotted in *Lysimachia quadrifolia* and *L. terrestris*. Of *L. vulgaris* there have been described three forms. The smallest, which grows in the shade, has light yellow flowers with greenish yellow filaments and is self-fertilized. The most conspicuous and largest form grows in sunny localities, has dark yellow petals with a red center and is rarely self-fertilized. The third form is an intermediate one. The flowers of *Lysimachia* are largely fertilized by bees of the genus *Macropis*. These pollen flowers, which attract few visits, display white, yellow, red, scarlet and blue colors, and the evidence is wholly insufficient to prove that the coloring has been determined by the selective agency of insects.

The species of *Primula*, well-known for the laborious investigations of Darwin, are largely dimorphous. The corolla is tubular and the honey is deeply concealed. The flowers are yellow and red. Bumblebees are frequent visitors to the yellow-flowered forms, and Müller found six red-flowered species in the Alps fertilized by butterflies. On *P. farinosa*, which is red with a yellow eye, he collected forty-eight species of *Lepidoptera*. In *Glaux* the corolla is wanting and the calyx is pink and petal-like. Sometimes the corolla is duplicated, as in the "hose in hose" flowers of *Primula acaulis*.

The Ebenales contain four families, the Sapotaceæ, Ebenaceæ, Symplocaceæ, and Styraceæ. There are but eight species in the Northern States, two with yellow and six with white flowers. In tropical regions these families are represented by a large number of trees and shrubs of which the most important is the ebony-tree, valued for its black heart wood.

The characters of the Gentianales and Polemoniales are so similar that the two orders cannot be readily distinguished. They differ from the preceding families, which are more closely allied to the Choripetalæ, in having but a single whorl of alternate stamens, and in the smaller number of carpels. Up to this point white and red colors have been most common in the Gamopetalous series, but these two orders are remarkable for containing a large number of purple and blue flowers.

The Gentianales include six families. The olive family, or Oleaceæ, contain two white, one purple and seven green flowers. The green flowers belong to *Fraxinus* (ash) and are the result of retrogression, as a part of the species have lost both calyx and corolla and are wind-fertilized, while others still retain the perianth. The common lilac (*Syringa vulgaris*) exhibits a great variety of beautiful shades including white, red, purple and blue. Showy yellow flowers occur in *Forsythia*.

The Loganiaceæ represent the stem-form of the order Gentianales. The presence of stipules distinguishes it from all of the other families of this order. The genera are synthetic in character and exhibit affinities in many different directions. Here are found the ancestral types of the Gentianaceæ, Apocynaceæ and Asclepiadaceæ, as well as of the Scrophulariaceæ and of the Rubiaceæ. The family is abundant in tropical regions but in the Northern States is represented by only four species; one of which is yellow, two white and one red. Our species are related most closely to the Rubiaceæ. The bird flower *Spigelia marilandica* (Maryland pinkroot) is scarlet outside, and yellow within, with a corolla one and one half inches in length, resembling in its coloring *Lonicera sempervirens*.

The Gentianaceæ are the first of the Gamopetalous families in which blue flowers are common. There are 7 white, 1 yellow, 10 red, 4 purple, and 16 blue flowers. The gentians form the most important genus. These plants many of which are characterized by a brilliant blue color are widely distributed in temperate regions, and are very abundant at alpine elevations extending upward to altitudes of over 15,000 feet. The genus contains white, yellow, red, purple and blue flowers. In the mountains of Switzerland the traveller is delighted by the vivid masses of blue coloring displayed by the gentians. Red-flowered species occur in the Andes. Müller regards *Gentiana lutea* as representing the primitive form of this genus. The rotate flowers are yellow with slender pointed petals, which are but slightly united. The honey is fully exposed to beetles and flies as well as to bees, but so few are the visitors that the plant is unable to dispense with spontaneous self-fertilization. The blue bell-shaped flowers have been evolved by bumblebees. The transi-

tion from yellow to blue is shown in *G. purpurea*, which is yellow inside and blue outside. A number of species by the lengthening and narrowing of the corolla have become adapted to Lepidoptera alone, or to bumblebees and Lepidoptera, but the blue color it is noteworthy has been retained. In the genus *Sabbatia* the handsome flowers are wheel-shaped, and the coloration seems to have changed from yellowish to white or pink, or pink-purple. *S. laucolata* and *S. paniculata* are white turning yellowish in fading; and *S. angustifolia* and *S. campanulata* are pink with a yellowish eye. Several of the rose-colored species are sometimes white. In *Erythraea* the slender funnel-form flowers are as the name of the genus denotes usually red. In *Frasera carolinensis* the rotate corolla is light greenish yellow with brown purple dots. *Bartonia* which grows in swamps and meadows shows evidences of retrogression in the thread-like stems and awl-shaped leaves. The flowers are small and white or yellowish.

The Menyanthaceæ are marsh or aquatic plants, which in our species have yellow or white flowers. The flowers of *Limnanthemum* (floating-heart) are short-lived. As the petals wither they become pulpy and exude a thin layer of liquid which is attractive to flies. A similar change occurs in *Tradescantia*.

The Apocynaceæ are confined chiefly to tropical regions. There are only seven species in the northern states but they exhibit a wide range of color, two are white, one yellow, one red, one purple and two are blue. The dogbanes (*Apocynum*) have small, bell-shaped, white, or pink flowers in cymes. The pinkish flowers of *A. androsaemifolium* are attractive to butterflies. The white species are visited by numerous bees. *Vinca minor*, or the myrtle, is blue, while *V. rosea* from the West Indies is rose or white. Both species are fertilized by bees. The Oleander (*Nerium*) cultivated from the Levant has large, scentless, showy rose-colored flowers that are fertilized by the hawkmoth *Sphinx nerii*. The caterpillar of this moth lives exclusively upon the leaves of the oleander. The species of this family in the north are too few to afford much information as to the relations of insects to their coloring.

Like the preceding family the Asclepiadaceæ are most abundant in the tropics. There are 11 white, 3 yellow, 5 red, 13

purple and 7 green flowers. The inflorescence is in umbels. Pollenization in the genus *Asclepias* is affected in a curious and remarkable manner, analogous in many respects to that of the *Orhidaceæ*. The pollen coheres in waxy masses called pollinia, which by means of an ingenious clip mechanism are clamped to the legs or antennæ of insects, and are thus transferred from one flower to another. When the pollinia come in contact with the stigma they adhere very firmly, and the insects obtain their freedom by snapping the connecting bands. Conspicuousness is gained by two whorls of petaloid bodies, the corolla and the corona. The corona is composed of five hood-shaped appendages bearing horn-like processes, within which the scented honey is plentifully secreted. The color of the corona is usually the same as that of the corolla, white, orange-red, or purple, though it is frequently of a different shade. But sometimes the flowers are distinctly bicolored; in *A. quadrifolia* the petals are pink and the corona is white, while in *A. lanceolata* the corolla is red and the corona orange. The visitors are Hymenoptera, butterflies and flies. Of the 22 northern species, 2 are greenish, 6 white, 3 yellow or orange, 4 red and 7 purple. The white and greenish-white flowers are the smallest. The two species of *Asclepiodora* have the corolla greenish and the hoods purplish. In *Acerates*, or green milk weed, the corolla is greenish and the hoods white, yellow, or purplish. In *Vincetoxicum* the corona is reduced to an annular ring adnate to the corolla, and the brown or red purple flowers possess a putrid odor attractive to carrion flies. The *Asclepiadaceæ* is one of the five Gamopetalous families, which contain seven or more greenish flowers. The prevalence of greenish and white flowers and the absence of blue would indicate that the coloring was but little developed in this family. The corona is perhaps analogous in its origin to the ligule of grasses.

The fifth gamopetalous order the Polemoniales, or Tubifloræ, is the largest and most difficult of this series. The families differ but little from each other, and are closely allied to the preceding order. About 900 species belong to the *Convolvulaceæ*, or morning-glory family, but they are confined chiefly to the tropics. In the Northern States this family contains 7 white,

1 yellow, 7 red and 3 blue flowers. The corolla is campanulate or funnelform. In *Ipomœa* and *Convolvulus* many of the flowers are bicolored, or tricolored. *Ipomœa purpurea* is purple, pink, variegated, or white, and a variety in my garden produced a purple flower striped with red, the whole flower fading to red. Both red and purple flowers may occur on the same plant. *I. versicolor* cultivated from Mexico has small, reddish flowers, which change to orange and yellow. *Convolvulus tricolor* has a blue corolla with a whitish throat and a yellow tube. The two species of *Quamoclit* have scarlet, salverform corollas adapted to humming-birds. The genus *Cuscuta* is a group of yellow, or orange-colored, parasitic plants destitute of chlorophyll, and of world-wide distribution. The flowers are white or tinged with rose. In Maine I have found that the visitors were small bees.

The Polemoniaceæ, or phlox family, are most abundant in the Western States. In the Eastern States there are 7 white, 10 red, 3 purple, and 8 blue flowers. The corolla of Phlox is salverform, and several of the red species have been observed to be fertilized by butterflies. *Phlox paniculata* and *P. drummondii* are favorites in cultivation for the brilliant effects they produce when massed. They have yielded innumerable shades and combinations of white, yellow, red and purple. A large number of the varieties are bicolored, in which the center may be white, red, purple, or even blue. A curious color variation of a perennial phlox of the variety Monsieur Maille is given in the *American Garden* for January, 1890. "In the morning the flowers were of a clear blue, remaining of this color until nearly noon, when they gradually changed to a delicate pink and by evening were a beautiful deep rose. This was repeated every day while the plant was in bloom." Many handsome red and blue flowers occur in the genus *Gilia*; in *G. tricolor* the lobes of the corolla are purple or white, and the throat brown purple, with a yellow tube. The genus *Polemonium* possesses pure blue flowers. In *Cobæa scandens* from Mexico the flowers are at first green changing to purple. Yellow is not common in this family. In the Polemoniaceæ, as in the Convolvulaceæ, the flowers are remarkable for the variety of their colors, for the number of combinations of two or more colors in a single flower, and for

the changes of color in individual flowers. These color relations will be again referred to under the Boraginaceæ.

Of the Hydrophyllaceæ 8 species are white and 10 blue. Frequently these latter species revert to white. They are mostly woodland flowers where blue contrasts with the yellowish or brown background. This is a small family intermediate between the preceding family and the Boraginaceæ.

The coloration of few families is so interesting as that of the Boraginaceæ, since the individual flowers often undergo several changes of color, and "seem to recapitulate to us the evolution of their colors." There are some 1500 widely distributed species. The inflorescence is in one-sided scorpioid spikes, racemes, or cymes. The flowers are small and regular, except in *Echium*, but the corolla varies much in length. In *Myosotis* and *Asperugo* the tube is short, and there is a great variety of visitors; while in *Borago* and *Symphytum* the flowers are inverted and the honey is accessible only to long-tongued bees. There are 6 yellow, 19 white, 1 purple and 17 blue flowers. *Heliotropum polyphyllum* is white but in variety *leavenworthii* of Florida bright yellow, and in *H. curassavicum* (sea-side heliotrope) the corolla is white with a yellow eye, changing to blue. Most of the species are, however, white or blue. The common heliotrope from Peru (*H. peruvianum*) has the tube white with the lobes purple, which in fading grow whitish. In this genus yellow and white appear more primitive than purple or blue. *Echinospermum* has small bell-shaped flowers, which are visited by flies, bees and moths. *E. lappula* in the bud is white, red before expanding, and afterwards bright blue. The coloration of *Myosotis*, one of the simpler genera, is remarkably variable. *M. palustris* and *M. laxa* are sky blue with a yellow eye; *M. arvensis* in bud has a yellow tube with pale pink corolla lobes, which change to blue and finally fade to white; *M. versicolor* is yellow changing to blue and violet, and *M. alpestris* produces dark blue, bright blue, reddish, and even snow white flowers. The flowers are visited by many species of flies. *Lithospermum purpureo-cœruleum* is at first purple-red and later blue. *Pulmonaria officinalis* is red and later blue-violet. *Echium vulgare* (blueweed) has large, showy, irregular flowers,

which change from red-purple to bright blue. *Symphytum officinale* has a yellowish-white corolla, which is rarely purplish. *Borago officinalis* has a bright blue corolla, with which the black cone of anthers offers a marked contrast. The last three species are fertilized chiefly by bees. To this family belongs *Arnebia cornuta*. When the flowers open each of the five petals is marked with a dark purple spot, which by the third day has faded entirely away leaving the corolla bright yellow. In the Boraginaceæ, it is evident, that yellow and white are more primitive than red, purple, or blue. A change in the cell sap from an acid to an alkaline condition explains the coloration of flowers, which are at first red but afterwards blue. The transition from yellow to blue may be caused by the development of a soluble blue pigment masking the yellow plastids, as in the purple pansy. The species of Boraginaceæ are very rich in anthocyan. The roots and in some instances the leaves and stems, as in *Echium* and *Lithospermum*, stain violet the herbarium paper on which they are mounted. From the roots of *L. canescens* (puccoon) the Indians derive a red dye. Another species of this family *Alkanna tinctoria* (alkanet) is extensively cultivated in Europe for its carmine dye used in coloring silk and cotton fabrics, and also oils, wax and wine. In the sheep pastures of New Mexico there grows another species *Plagiobothrys arizonicus*, called blood purslane, "when the sheep find a patch of it, it colors their heads red clear to the ears."¹

The flowers of the Verbenaceæ are two-lipped. Of the 12 northern species, two are white, two purple and eight blue. The species present various interesting color changes and combinations of colors. The native species of *Verbena* are white, purple, or blue. The cultivated varieties are remarkable for their brilliant scarlet and crimson colors. *Lantana mixta* from Brazil has flowers, which at first are white changing to yellow, orange and finally to red. According to Fritz Müller, the flowers when yellow are sought by bees, and when red by butterflies. *L. nivea* has sweet-scented white flowers, which in the variety *L. mutabilis* change to bluish. The flowers of *Clerodendron* are

¹ Norton. *Report Missouri Botanical Garden*, 1898, p. 149.

bicolored with the calyx and corolla strongly contrasted; *C. trichotomum* from Japan has a white corolla and a red calyx, while *C. thomsonæ* from tropical Africa has a snow white calyx and a bright crimson corolla.

The Labiatæ is a large family of about 3000 species of widely distributed plants, which are especially abundant in the region of the Mediterranean. The foliage usually contains an aromatic volatile oil. The flowers are distinctly zygomorphous, and highly specialized both in form and color. In this family and the Scrophulariaceæ the gamopetalous plants come to a secondary culmination. But while these two families belong to the same order they are in different subseries, and are more closely united with other families than with each other. The Labiatæ connect with the Verbenaceæ, both having one-ovuled carpels; and the Scrophulariaceæ are related to the Solanaceæ, both having carpels with numerous ovules.

The 120 species of the Labiatæ contain 24 white, 4 yellow, 12 red, 47 purple and 33 blue flowers. According to the length of the corolla tube and the consequent limitation of the insect visitors, the flowers may be arranged in three groups. In *Mentha* and *Lycopus* the tube is short, and the visitors are chiefly flies. In *Thymus*, *Origanum* and *Betonica* bees become of increasing importance, though flies and other insects are also numerous. While *Stachys*, *Ajuga*, *Teucrium*, *Salvia*, *Lamium*, *Galeopsis* are almost exclusively fertilized by bees. Individually the flowers are often inconspicuous and significance is gained by massing. In *Mentha* and *Lycopus* the stamens are reduced to four or two, the nearly regular corolla is 4-lobed, and the small, pale purple or white flowers, which are fertilized chiefly by flies, are in dense axillary whorls. These genera have evidently retrograded and departed from the typical labiate form. The flowers of *Lycopus* are the smallest of this family. The small flowers of *Thymus* and *Origanum* are in terminal clusters, 2-lipped with a five-cleft corolla. In both genera there occur large hermaphrodite and small pistillate flowers. The color is purple and the visitors are flies, bees and butterflies, but the largest percentage is of flies. The flowers of *Koëlia* (*Pycnanthemum*), or basil, are more or less bilabiate. They are small,

white, or purple-dotted, and for the most part are in terminal clusters. The species, like the mints, are strongly aromatic-scented. In many purple-flowered species of the Labiate family the leaves and stems also develop a purple pigment, as in *Mentha* and *Origanum*. The entire plant of the summer savory (*Satureia hortensis*) turns purple in autumn, while on the other hand the white-flowered water horehound (*Lycopus*) has pale green foliage.

A great number of the larger labiate flowers are chiefly, or almost exclusively, fertilized by bees. A number of species, however, have scarlet flowers and are adapted to humming-birds. The species of *Stachys* are white, yellow, red, or purple, and the lower lip is frequently spotted or variegated. The flowers are rather large and bees are the most important pollinators. The flower of *S. recta* is yellowish-white with the border of the upper lip marked with two purple stripes, and the lower lip purple spotted. *S. annua* has the corolla tube whitish-yellow with the lower lip red-spotted. The corolla of *S. palustris* is bright purple with a white and dark red marking on the under lip, and the flower of *S. silvatica* is red with a purple and white pathfinder on the lower lip. Our four northern species of *Lamium* are pollenized for the most part by bumblebees. Three are purple or purple-red and one is white. The under lip is variegated. *L. album* is large, white, or sometimes rose-colored, with the under lip pale yellow, marked with olive-colored dots. The pathfinders of the purple-red *L. maculatum* are dark red with white markings, and of the bright purple *L. purpureum*, a dark red flake and dark red lines.¹ The flowers of *Galeopsis*, or hemp-nettle, display as great a variety of colors. *G. tetrahit*, so common in waste places, is purple with a pathfinder on the lower lip of a yellow spot crossed by a network of red lines; while *G. versicolor* is yellow with the lower lip in front dark violet but at its base yellow. The species of *Prunella* are also bee flowers; *P. vulgaris* is blue-purple, white, or rose-colored. *Salvia pratensis* is usually purple, but Müller mentions a pink variety grown in his garden. *Ajuga reptans* is a bumblebee flower, and also

¹Knuth, Paul. *Handbuch der Blütenbiologie*, bd. ii, teil 2, p. 259.

has blue, rose, or white flowers. The native species of *Salvia* are blue, or blue and white, and are fertilized by bumblebees. But in tropical America there occur scarlet and fire-red species, which are visited by humming-birds. Further illustrations of variegation may be observed in *Teucrium*, *Scutillaria*, *Nepeta* and *Monarda*. It will be noted that the bee flowers are larger and more variable in color than the species to which flies are the most important visitors. Bee fertilization is correlated with high specialization in form and color. Pathfinders usually occur on the lower lip and consist of two, three, or even four colors, one of which is very frequently yellow. The Labiatæ have but four yellow flowers, while the Scrophulariaceæ have thirty-three. These four species are pale or greenish-yellow, as in *Lophanthus nepetoides*. The colors of the Labiatæ will again be considered under the Scrophulariaceæ.

The Solanaceæ, or potato family, belong to the same sub-series as the Scrophulariaceæ, or figwort family. The flowers of the Solanaceæ are regular or nearly so, and the corolla tube varies greatly in length from rotate and campanulate to salverform. There are five perfect stamens of equal length. This family represents an earlier stage of the Scrophulariaceæ. *Petunia* is a transition form, which has the border unequal and four of the stamens didynamous and the fifth aborted. Many species of *Linaria*, a well known genus of the Scrophulariaceæ, have been known to become regular.¹ A peloric form of *Antirrhinum majus* is also known. Moreover at an early stage in their development the flowers of the Scrophulariaceæ are regular.

Nine species of the Solanaceæ are white, twenty-one yellow, two purple, and eight blue. The genera *Lycopersicum* (tomato) and *Solanum* (nightshade) contain pollen flowers, and are devoid of honey. They are visited sparingly by both bees and flies. The rotate flowers of *Solanum* are white, yellow, purple and blue with a cone of yellow anthers in the center, or in *S. heterodoxum* the lowest anther is violet like the corolla. The violet corolla of *S. dulcamara* (nightshade) is marked at the base with ten green spots, which Müller observed Syrphidæ

¹ Darwin. *Animals and Plants under Domestication*, vol. ii, p. 35.

examining in search of nectar. The fruits of this genus are green, white, yellow and red. The small, open, campanulate flowers of *Physalis* (ground-cherry) are nectariferous. The seventeen northern species are greenish-yellow, bright yellow, or sulphur-yellow, sometimes throughout, but often with a brown or purple center, or with purplish spots. The yellow anthers are frequently tinged with purple, and the calyx in some species is purple-veined. The berry is also yellow or purple. In *Leucophysalis* the flower is white sometimes tinged with purple with a yellow center. The fruiting calyx of the strawberry tomato, *P. alkkekengi* from Southern Europe, contains an intense scarlet pigment.

The flowers of *Nicotiana* and *Datura* are funnelform, or tubular, and adapted to Lepidoptera. *Nicotiana rustica* and *N. longiflora* are nocturnal species; in the former the corolla is yellowish-green, and in the latter it has a white border and a green tube four inches in length. The common tobacco, or *N. tabacum*, which is a diurnal species, has red-purple flowers. In *Datura* the large nocturnal flowers are four inches long by two broad. *D. stramonium* has green stems and white flowers, while *D. tatula* has violet-purple flowers and purple stems. *Brunfelsia grandiflora* has greenish flowers two inches in length; while *B. latiflora* has lavender flowers with a white eye, which fade to white. Both of these species come from South America. Two cultivated exotic genera, which also have funnelformed corollas, are *Salpiglossis* and *Petunia*. The large handsome purple or rose-colored flowers of *Salpiglossis* are remarkable for being netted-veined and laced with golden yellow. The numerous hybrids of *Petunia* under cultivation are chiefly derived from two South American species, one of which is white and the other red-purple. They exhibit a wonderful variety of bicolored, tricolored, and variegated flowers often veined or mottled in endless ways. A unique form is striped or margined with green. The coloration of the *Solanaceæ*, which is an extensive tropical family, is of more than usual interest because of the many green flowers of large size which it contains. These green flowers, as well as many large white and yellow colored species, are funnel-form or tubular, most strongly sweet-scented in the evening and

adapted to night-flying Lepidoptera. Nocturnal fertilization has prevented the development of red and blue colors, as in *Cestrum nocturnum* with yellowish green, *C. parqui* with dull yellow, *Datura metel* with white, and *D. fastuosa* with the flowers violet outside and white within. *Cestrum elegans* and *Nicotiana tabacum* are day flowers and are rose purple. Of the bumblebee flowers, *Atropa belladonna* is dull purple, and *Hyoscyamus niger* is dull yellow with purple veins. The colors of the rotate flowers of *Solanum* and *Physalis* are white, yellow, purple and blue, and are sought by both bees and flies.

Unlike the Solanaceæ the Scrophulariaceæ are most abundant in temperate and arctic regions. There are about 2500 species. Of the 113 northern flowers, 13 are white, 33 yellow, 7 red, 32 purple, and 28 blue. As in the Solanaceæ the number of yellow flowers is much larger than in the Labiatae. In *Verbascum* and *Veronica* the flowers are wheel-shaped. Three of the northern species of *Verbascum*, or mullein, are yellow or sometimes white. Gärtner made many experiments in crossing the yellow and white varieties, and actually raised one variety from the seed of the other.¹ *V. phaniceum* is purple, rose-colored, or white. When the purple variety of *V. phaniceum* was crossed by the yellow variety of *V. blattaria*, the corolla of the hybrid was pale crimson.² The leaves of *Verbascum thapsus* are yellowish green, often spotted with yellow, or turning completely yellow. The visitors are a miscellaneous group of insects, of which bees are the most important. Müller devotes considerable space to the consideration of the colors and manner of fertilization of the speedwells, or the genus *Veronica*. Most species have light or dark blue flowers often with darker stripes; but those of *V. urticifolia* and *V. perigrina* are pink. The flowers, which are small and rotate, with the sepals and petals reduced to four and the stamens to two, have evidently departed widely from the primitive type of the family. The visitors are chiefly flies, especially Syrphidæ, the honeybee and the smaller bees. Müller finds it difficult to explain the origin of the blue coloring by the

¹ Darwin. *Animals and Plants under Domestication*. Vol. ii, p. 83.

² Kerner. *Natural History of Plants*, vol. ii, p. 567.

selective influence of the pollenizers, and regards the question of its evolution as still unsolved. It is surprising that he does not give more consideration to the influence of physiological, as well as of ecological causes, in determining the particular colors of flowers. In this genus, as in many others, it is the character of the pigment-forming function, which is of chief importance. On the Alps Müller found *Tossia alpina* to be also a fly flower. The corolla is bright yellow except that the three lower petals are spotted with dark purple. In view of the fact that fly-flowers are white, yellow, red and blue, the evidence that their particular coloration has been determined by the color sense of Diptera must be regarded as unsatisfactory.

The species of *Scrophularia* are wasp flowers, green or purplish without and brown purple and shining within. The corolla is short and round with easily accessible honey. By far the greater number of species of the *Scrophulariaceæ* are adapted to bees and many to bumblebees alone. The species of *Linaria* are for the most part bumblebee flowers. *L. vulgaris* is bright yellow with an orange-colored palate as a honey-guide, while *L. canadensis* has small blue flowers with a whitish palate. *Antirrhinum majus* is bright purple or white with a yellow palate. *A. crontium*, according to Knuth, is red, or rarely white, with darker red lines. The under lip displays a pale yellow pathfinder and a white zone besides other markings. *Chelone glabra* (turtle head) is white with reddish lips. In Maine this species is fertilized exclusively by bumblebees. *C. obliqua* is bright rose color. *Digitalis purpurea* is purple with dark purple spots within on the lower side. *D. lutea* is yellow. *Melampyrum lineare* is whitish with the lower lip yellow. Other species of this genus have bright yellow flowers. *Pedicularis* with the flowers yellow and red is also fertilized by bumblebees. *Rhinanthus crista-galli* (yellow rattle-box) is bright yellow with the lower lip purple-spotted.

In a preceding paper the capability of the calyx to develop different colors was shown to equal that of the corolla. In connection with the genus *Castilleja* the variety of coloring in the floral bracts may be considered with advantage. In *C. coccinea*, or the scarlet painted cup, the flower is greenish yellow and the

floral bracts bright scarlet, or occasionally both bracts and calyx are yellow. In *C. indivisa* both bracts and calyx are bright red, and in *C. acuminata* yellowish or purplish, but in *C. sessiliflora* they are green similar to the leaves. In *Monarda didyma* of the Labiatae the corolla is scarlet and the bracts red, in *M. media* both are purple; but in *M. clinopodia* the bracts are pale or white, and the flower is yellowish-pink. In *Cornus canadensis* the involucre is white and white or red in *C. florida*. *Bourgainvillea glabra* has three conspicuous purple-red bracts. Finally in the Proteaceae *Protea globosa* has "the upper foliage leaves grouped into a large outer envelope, which surrounds the spherical golden yellow inflorescence, and these crowded leaves are colored blue in contrast to the lower scantier foliage which has a grass green color." Other illustrations of colored floral bracts occur in the aroids, spurges and Compositae. The floral bracts evidently may develop as wide a range of colors as the floral leaves, though blue is much rarer.

Müller in his *Alpenblumen* has considered the relation of bees to floral colors at considerable length. In many genera, when the flowers are wheel-shaped and adapted to short-tongued visitors, the species are colored alike, mostly yellow or white, as in *Ranunculus* and *Potentilla*, the Alsineae, Cruciferae and Umbelliferae. Even when the honey is partially concealed this may hold true, as in *Mentha* and many Cichoriaceae and Compositae. The short-tongued insects visit these flowers indiscriminately and not infrequently the bees. Genera adapted to bees on the contrary usually display a variety of colors, as white, yellow, red, violet, blue and brown, especially when they bloom in the same locality at the same time. Among the examples given by Müller are *Aconitum lycoctonum* yellow, *A. napellus* blue; *Lamium album* white, *L. maculatum* red, *Galeobdolon luteum* yellow; *Salvia glutinosa* yellow, *S. pratensis* blue; and *Pedicularis tuberosa* whitish yellow and *P. verticillata* purple. An exception to this rule is offered by the Papilionaceae, which contain a great number of yellow flowers. Here Müller thinks that the color is so strongly transmitted that not even small variations appear, and there is consequently no opportunity for the development of a variety of colors. As a rule, however, genera

with rotate open flowers are monochromatic, while genera with highly specialized corollas adapted to bees are polychromatic. How have these color differences arisen, and how far are they due to the selective influence of bees? That bees in collecting nectar adhere closely in their visits to a single species is well known. Even when the flowers are nearly alike in form and color the honeybee often shows a remarkable power of discrimination. If all of the flowers blooming at the same time in a locality were of the same color, it is evident that bees could not distinguish between them as readily as when there is a variety of colors contrasting with each other. This is the reason of the development, according to Müller, of the numerous color differences in bee flowers. There can be no doubt that bees can distinguish between different hues, and can make their visits more quickly and easily because of the contrasts of flowers in coloration. If, says Müller, we assume that one of two forms, closely allied in structure and of the same color, should vary in color, bees would distinguish it at once, and follow it more easily in their visits. He found, moreover, that a majority of bee flowers are red or blue. Of one hundred species of bee flowers observed by him on the Alps thirty-four were white or yellow, and sixty-six red or blue. In the German and Swiss flora he records that 152 bee flowers were white or yellow, and 330 red, violet, or blue. The honeybee and bumblebees showed a much larger percentage (about 20 %) of visits made to red and blue flowers of all kinds, including not only flowers with the honey partially or deeply concealed but also those with it fully exposed, than to white and yellow flowers. To explain the greater frequency of their visits to red and blue flowers, it does not seem to the writer necessary to assume that they find greater pleasure in these hues. The more specialized bees learn from experience, and it is not difficult to understand that they would soon come to associate with red and blue colors a more abundant supply of nectar and greater freedom from competition.

(To be continued.)